

TENTACLE RETRACTION IN TRACHEOPULMONATA*

By

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Text-figs. 1-7

The position of the eyes and the method of withdrawal of the tentacles of pulmonate gastropods have been observed by various workers for many years. The fundamental importance attributed to the position of the eyes in regard to the tentacles may be seen in the names of the two most prominent pulmonate orders, STYLOMMATOPHORA Schmidt (1855) and BASOMMATOPHORA Keferstein (1864). Snails of the order Basommatophora, mostly freshwater inhabitants (but some taxa live in the sea, and a few are essentially land snails), have their eyes at the bases of the single pair of tentacles. Snails of the order Stylommatophora, all basically land inhabitants, have their eyes on the tips of the upper and larger pair of tentacles†. An additional noteworthy difference between these two groups in regard to their tentacles is in the musculature responsible for tentacle retraction. Tentacles of the Basommatophora, on direct physical stimulation, withdraw by simply shortening and thickening (Fig. 1). The tentacles of the Stylommatophora, on the other hand, are withdrawn by a progressive inversion beginning at the distal end and proceeding proximally (Fig. 2).

Sarasin & Sarasin (1899), after studying the anatomy and embryology of the Veronicellidae, concluded that these terrestrial slugs had descended from shelled gastropods which were neither Basommatophora nor Stylommatophora, but shared features of both of these groups as they are known today. Members of this family have their eyes placed at the tips of the upper pair of tentacles, like the Stylommatophora, but they retract them similarly to the Basommatophora, i.e., by contraction (Fig. 3). Pilsbry (1948) proposed the order SYSTELLOMMATOPHORA for this group of slugs (together with the onchidellids), and placed as first importance the method of withdrawal of the tentacles ("Pulmonata

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† The only apparent exceptions to this condition in the Stylommatophora are in the Athoracophoridae and the Pupillidae (see Pelseneer, 1897 and Pilsbry, 1948). The Athoracophoridae, and among the Pupillidae, *Columella* and *Pupisoma*, have only one pair of tentacles (the upper pair), and the pupillid *Vertigo* is apparently totally without tentacles.

in which the eyes are on contractile (not inversible) stalks"*). He included as synonyms the following: *Ditremata* Fischer (1883), *Teletrema* Pilsbry (1898), *Digonopora* Suter (1913), and *Onchidiacea* and *Soleolifera* Thiele (1931).

The importance in current taxonomic schemes given to the position of the eyes in regard to the tentacles, and the method of withdrawal of the tentacles, induced me to present my observations on the tentacular characteristics of several species of the odd South Pacific land slug family Athoracophoridae, since their method of tentacle withdrawal has not been stressed in previous literature. This method differs basically from that found in other pulmonate snails, and especially from that found in the Stylommatophora, where they are usually placed.

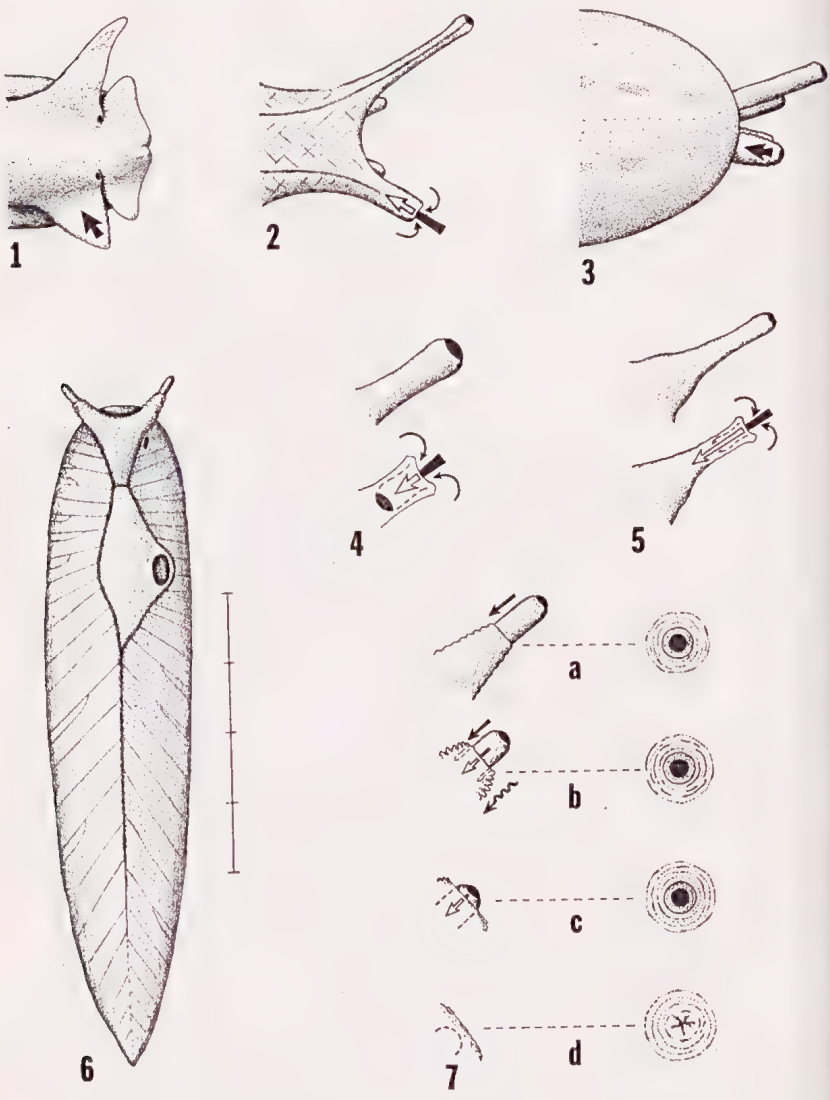
Simroth (1890, *vide* Solem, 1959) proposed the taxon TRACHEOPULMONATA for the athoracophorid slugs, which possess the anomalous "lung" that has been compared by Simroth and others to the tracheal system of insects. The presence of only one pair of tentacles in this aberrant group was noticed as early as 1832 by Quoy and Gaimard, who named a New Zealand slug *Limax bitentaculatus* (the type species of Gould's (1852) genus *Athoracophorus*, on which Fischer (1883) based his family Athoracophoridae). Others have made note of tentacular retraction in tracheopulmonate slugs. For example, Gray (1860) included the "Aneiteadae" and "Janelladae" [Athoracophoridae] in his group A of the "Pulmonata geophila", distinguished by "head, eye-peduncle, and tentacles retractile under the skin," in contrast to his group B ("Vermicellidae" and "Onchidiadae") in which the "head, eye-peduncle, and tentacles [are] simple, contractile." Hedley (*vide* Pfeiffer, 1900) described the tentacles of his *Aneitea* from Brisbane as contractile and retractile. Glamann (1903) characterized (in part) the Janellidae as having two tentacles, which can be invaginated by several retractors and carry eyes on a terminal knob. Suter (1913) noted that in *Athoracophorus papillatus* "the anterior half [of the tentacles are] narrower than the posterior, and telescoped into the latter when retracted". Thiele (1931) said of the Tracheopulmonata, "Kopf mit 2 augentragenden, einstülpbaren Fühlern . . ." None of these descriptions precisely characterize tentacle retraction in *Aneitea* as described in the present paper, although Hedley's and Suter's are the most accurate, as brief as they are.

My observations were made on many living specimens of several species of *Aneitea* from Éfaté, Malekula and Tanna Islands while I was in the New Hebrides in January and February, 1967. Specific determinations of the material are not given here because of the present uncertainty regarding identification. Assignment of specific names must await a detailed anatomical study of my specimens, and comparisons with Grimpe & Hoffmann's (1925) material. Solem (1959) pointed out the difficulty of species discrimination in New Hebridean athoracophorid slugs. However, exact species determinations are not important for the purposes of the current paper, since the observed behaviour of tentacle retraction was the same for all specimens examined.

In New Hebridean *Aneitea* species the anterior and posterior (or distal and proximal) portions of the tentacles are clearly demarcated. The anterior portion is rod-like with the eye at its tip (Fig. 7a). The posterior part is ordinarily somewhat concentrically furrowed and

* However, at least the genera *Onchidella* and *Onchidium* of the Onchidiacea have invaginable rather than contractile tentacles (Figs. 4, 5) (see also Plate, 1893).

tapers outward to its base. When the tentacle is retracted, the anterior part does not contract, but is pulled into the posterior part, which contracts by an accordion-like pleating (Fig. 7b). As retraction continues, the anterior part is pulled further into the posterior part, which itself (after being completely folded) begins to be pulled into the body wall. At a point of near extreme contraction, before the tip of the anterior peduncle disappears within the snail's head, the eye at the tip is clearly observable (Fig. 7c), and not inverted, as is the case in



the other Stylommatophora. On extreme retraction, the eye disappears within the body wall (Fig. 7d), still not inverted. As the eye stalk begins to reappear as the tentacle is again pushed out, it can clearly be seen that the eye has not inverted within the anterior peduncle.

As shown in Fig. 7, the tentacles of *Aneitea* are not "inversible" or "introvertible" (in the sense those terms have been used for the Stylommatophora), nor are they "contractile" (in the sense of the Basommatophora and Soleolifera). However, the proximal portions of the tentacles can be contracted and, along with the eye stalk, invaginated into the snail's anterior body. But, the distal eye stalk itself is not inverted, and the eye remains at its tip until it is finally withdrawn into the invaginating lower portion of the tentacle. Thus, in this respect the tentacles of this genus, and presumably those of other Tracheopulmonata, exhibit a significant and perhaps basic difference from the completely invertible tentacles of all Stylommatophora known to me, including the Succineidae (which are sometimes considered to be related to the Tracheopulmonata). The tentacles of *Aneitea* also differ from the other pulmonate groups: the Basommatophora, Soleolifera and Onchidiacea (Table 1).

Plate (1898), Simroth (1920) and others, although not precisely describing tentacular retraction, have pointed out the basic differences in the tentacular retractor muscles of tracheopulmonate slugs from those known in the Stylommatophora.

It is concluded from these brief observations that, if tentacular structure and mode of tentacle retraction are given importance in dividing the orders of the Pulmonata, then these characters, together with the other known gross differences between the Athoracophoridae and the Succineidae (including a holopod foot in the former and an aulacopod foot in the latter), indicate that the tracheopulmonate slugs are not closely related to the stylommatophoran succineids, and should not be included as a subfamily of the Succineidae as advocated by Cockerell (1891), or perhaps even together with them in the Heterurethra as has been suggested by Baker (1955). Pilsbry (1948) reached a similar conclusion about their taxonomic placement, i.e., that the Tracheopulmonata should be considered as a separate order removed from the Heterurethra.

TEXT-FIGS. 1-7. Types of tentacle retraction in Pulmonata

1. Basommatophora [*Radix auricularia* (Linnaeus), Detroit, Michigan, U.S.A.]
2. Stylommatophora [*Triodopsis* sp., Ann Arbor, Michigan, U.S.A.]
3. Soleolifera [*Veronicella floridana* (Leidy), Florida, U.S.A.]
4. Onchidiacea [*Onchidella evelinae* Marcus & Burch, Marshall Islands]
5. Onchidiacea [*Onchidium* sp., New Hebrides]
- 6-7. Tracheopulmonata [*Aneitea* sp., New Hebrides]
6. Dorsal view of slug.
7. Progressive degrees of tentacle retraction are shown in a-d. Lateral views are shown in the left column, and corresponding dorsal views of the retracting tentacle are shown in the right column.

Measurement line (in cm) is for Fig. 6 only. Figs. 2-3 are from Burch (1962).

TABLE 1

Taxa	Pairs of tentacles	Location of eyes in relation to tentacles	Type of tentacle retraction	Complete withdrawal of eye into body
Basommatophora	1	base	contractile	No
Soleolifera	2	tip	contractile	No
Onchidiacea	1	tip	inversible	Yes
Stylommatophora	2	tip	inversible	Yes
Tracheopulmonata	1	tip	contractile and invaginable	Yes

TABLE 1. Tentacle characteristics of pulmonate snails.

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